



TABLE 4. Mean (Min.-Max.) genetic distance

Species	1. <i>C. castaneus</i>	2. <i>C. sp.</i>	3. <i>C. laevis</i> , 10*	4. <i>C. laevis</i> , 11**	5. <i>C. heptacanthus</i>	6. <i>C. urotaenia</i>
1.	0.003 (0.000-0.007)	0.160 (0.145-0.175)	0.204 (0.187-0.221)	0.210 (0.186-0.226)	0.502 (0.473-0.523)	1.565 (1.541-1.587)
	2.	0.001 (0.000-0.001)	0.114 (0.113-0.115)	0.198 (0.194-0.201)	0.478 (0.474-0.482)	1.573 (1.546-1.591)
		3.	—	0.194 —	0.311 —	1.568 (1.558-1.575)
			4.	—	0.375 —	1.395 (1.372-1.425)
				5.	—	1.315 (1.294-1.335)
					6.	0.008 (0.002-0.018)
						7.

\*; Lake Hatirou-gata. \*\*; Koma River.

TABLE 5. Estimates of genetic variability in genus *Chaenogobius*

Species	Population No.	No. of alleles per locus	% polymorphic loci	Average heterozygosity (expected)
<i>C. castaneus</i>	1	1.467	26.7	0.061
	2	1.267	20.0	0.052
	3	1.267	13.3	0.043
	4	1.067	6.7	0.031
	5	1.200	20.0	0.061
	6	1.133	13.3	0.052
	Mean	1.234	16.7	0.050
<i>C. sp.</i>	7	1.133	13.3	0.033
	8	1.200	6.7	0.036
	9	1.067	6.7	0.023
	Mean	1.200	8.9	0.031
<i>C. laevis</i>	10	1.467	26.7	0.058
	11	1.067	6.7	0.027
<i>C. heptacanthus</i>	12	1.200	6.7	0.022
<i>C. urotaenia</i>	13	1.067	6.7	0.015
	14	1.067	6.7	0.015
	15	1.067	6.7	0.033
	16	1.133	13.3	0.048
	Mean	1.084	8.4	0.028
<i>C. sp.1</i>	17	1.200	0.0	0.010
<i>C. sp.2</i>	18	1.067	6.7	0.009
	19	1.067	6.7	0.013
	20	1.067	6.7	0.015
	21	1.067	6.7	0.006
	22	1.067	6.7	0.012
	Mean	1.067	6.7	0.011
<i>C. isaza</i>	23	1.200	13.3	0.062
Overall mean		1.157	10.7	0.032

between *Chaenogobius* species

7.	8.	9.
<i>C. sp. 1</i>	<i>C. sp. 2</i>	<i>C. isaza</i>
1.286 (1.272-1.301)	1.570 (1.545-1.589)	1.529 (1.531-1.562)
1.310 (1.305-1.319)	1.577 (1.549-1.593)	1.554 (1.535-1.566)
1.290 —	1.574 (1.566-1.577)	1.549 —
1.146 —	1.376 (1.372-1.386)	1.352 —
1.301 (1.296-1.306)	1.593 (1.591-1.595)	1.567 —
0.237 (0.227-0.249)	0.225 (0.206-0.252)	0.103 (0.092-0.120)
—	0.414 (0.401-0.412)	0.358 —
8.	0.000 (0.000-0.001)	0.235 (0.232-0.242)
	9.	—

should supply significant information to establish the taxonomic relationship between them.

Three species of *C. urotaenia*, *C. sp. 1* and *C. sp. 2* were confirmed that they were different species each other. Genetic distances between them ranged from 0.225 to 0.412 on average. These values are large, indicating that they are different species. *C. urotaenia* and *C. sp. 2*, distributing sympatrically at the four rivers in the Shimane Prefecture, had different alleles at the *Sod* locus and at the *Mdh* locus from each other and no heterozygote at these loci was observed through this study. Ecological study also showed that they are ethologically isolated [10].

This study revealed phylogenetic position of *C. isaza* which is specialized to land-locked freshwater and endemic to Lake Biwa. It was closely related to *C. urotaenia*, amphidromous species as previously suggested [11]. We used the estimation of divergence time from genetic distance proposed by Nei [18],  $t=5 \times 10^6 D$ . It suggested that *C. isaza* was differentiated from *C. urotaenia* about 0.5 million years ago. This time agrees with the origin of other endemic species in Lake Biwa, which was suggested by fossil records [25, 26]

Isozyme polymorphisms supplied the information on population system in some species. The comparison between populations within three amphidromous species, *C. castaneus*, *C. urotaenia* and *C. sp. 2*, showed that the differentiation of populations did not reflect the geographic distance between populations from different rivers (data was not shown). This suggests that genetic mixture between populations occurs when larvae go down to the sea and they have no behavioral character to return to the river where they were born. This study indicates the effectiveness of application of isozyme polymorphism to ecological study of *Chaenogobius* species that have various life histories.

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## REFERENCES

- 1 Akihito, Prince (1984) Genus *Chaenogobius*. In "The Fishes of the Japanese Archipelago". Ed by H Masuda, H K Amaoka, K C Araga, T Ueno, T Yoshino, Tokai University Press, Tokyo, pp 264-266 (in Japanese)
- 2 Avise J C (1974) Systematic value of electrophoretic data. *Syst Zool* 23: 465-481
- 3 Avise J C (1976) Genetic differentiation during speciation. In "Molecular Evolution Vol. 7" Ed, by F J Ayala, Sinauer. Sunderland, Mass; pp 106-122
- 4 Ayala F J (1975) Genetic differentiation during the speciation process. *Evol Biol* 8: 1-78
- 5 Ayala F J, Tracy M L, Hedgecock D, Richmond R C (1974) Genetic differentiation during the speciation process in *Drosophila*. *Evolution* 28: 576-592
- 6 Buth D G (1984) The application of electrophoretic data in systematic studies. *Ann Rev Ecol Syst* 15: 501-522
- 7 Dotu Y (1955) The life history of a Goby, *Chaenogobius urotaenia* (Hilgendorf). *Sci Bull Fac Agr Kyushu Univ* 15: 367-374
- 8 Clayton J W, Tretiak D N (1972) Amine-citrate buffers for pH control in starch gel electrophoresis. *J Fish Res Bd Canada* 29: 1169-1172
- 9 Hayashi M, Sato H (1987) One species of genus *Chaenogobius* from Shinji Lake, Shimane prefecture. *Proc Ann Meet Japan Ichthyol Soc* 48 (abstract in Japanese)
- 10 Ishino K (1987) Freshwater fishes in Japan, their distribution, variation and speciation. Ed by M, Mizuno, A Goto, A Tokai Univ Press, pp 189-197 (in Japanese)
- 11 Kawanabe H (1978) Some biological problems. *Verh Internat Verein Limmol* 20: 2674-2677
- 12 Koshikawa T (1989) Shinjiko-haze, *Chaenogobius* sp. In "Freshwater Fishes of Japan" Ed by H, Kawanabe, N Mizuno, Yama-Kei Publishers Co., Ltd., pp 614-615 (in Japanese)
- 13 Koshikawa T, Sato H (1986) Synopsis of new recorded goby, *Chaenogobius* sp. of Lake Shinji. *The Freshwater Fishes*, 12: 51-55 (in Japanese)
- 14 Masuda Y, Ozawa T, Enami S (1989) Genetic differentiation among eight color types of the fresh water goby, *Rhinogobius brunneus*, from Western Japan. *Japan J Ichthyol* 36: 30-41
- 15 Nakanishi T (1978) Comparison of color pattern and meristic

- characters among the three types of *Chaenogobius annularis* Gill. Bull Fac Fish Hokkaido Univ 29: 223-232
- 16 Nei M (1972) Genetic distance between populations. Am Nat 106: 283-292
  - 17 Nei M (1975) Molecular Population Genetics and Evolution. North-Holland Pub.Co., Amsterdam
  - 18 Nei M (1987) Molecular Evolutionary Genetics. Columbia University Press, New York
  - 19 Nevo E, Beliles A, Ben-Shlomo R (1984) The evolutionary significance of genetic diversity: Ecological, demographic and life history correlates. In "Evolutionary Dynamics of Genetic Diversity" Ed by G S Mani, Springer-Verlag, pp 13-213
  - 20 Numachi K (1981) A simple method for preservation and scanning of starch gels. Biochem Genet 19: 233-236
  - 21 Numachi K, Nagahora S, Iwata M (1979) Genetic demonstration of hybrids between chum and pink salmon in the northwest Pacific. Rep Otsuchi Mar Res Cent Univ Tokyo 5: 87-102
  - 22 Pasteur N, Pasteur G, Bonhomme F, Catalau J, Britton-Davidian J (1988) Practical Isozyme Genetics. Ellis Horwood limited, England
  - 23 Pinchuk V I (1978) Notes and supplements to the Family Gobiidae in the book by Lindberg and Krasnyukova "Fish of the Sea of Japan and the neighboring part of the Sea Ohotsk and the Yellow Sea", Part 4, 1975 with a description of new species *Chaenogobius taranetzi*. J Ichtyol 18: 1-14
  - 24 Powell J R (1975) Protein variation in natural populations of animals. Evol Biol 8: 79-119
  - 25 Research Group of Natural History of Lake Biwa (1983) Fossil assemblages from the Pleistocene Katata formation of the Kobiwako group at Ogi-cho, Otsu City, Central Japan. Bull Mizunami Fossil Museum 10: 117-142
  - 26 Research Group for Natural History of Lake Biwa (1986) Freshwater fossil assemblage from the Pleistocene Kobiwako group on the southwest side of Lake Biwa Bull. Mizunami Fossil Museum 13: 57-103
  - 27 Richardson B J, Baverstock P R, Adams M (1986) Allozyme Electrophoresis. Academic Press, Australia
  - 28 Selander R K, Smith M H, Yang S, Johnson W E, Gentry J B (1971) Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud Genet 6 Univ Texas Publ 7103; 49-90
  - 29 Shaw C R, Prasad R (1970) Starch gel electrophoresis of enzymes-A compilation of recipes. Biochem Genet 4: 297-320
  - 30 Sneath P H A, Sokal R R (1973) Numerical Taxonomy. Freeman, San Francisco, pp 188-308
  - 31 Takagi K (1952) A critical note on classification of *Chaenogobius urotaenia* and its two allies. Japan J Ichthyol 2: 14-22
  - 32 Takagi K (1966a) Taxonomic and nomenclatural status in chaos of the Gobiid fish, *Chaenogobius annularis* Gill I. Review of the original description, with special reference to estimation of the upper jaw relative length as a taxonomic character. J Tokyo Univ Fish 52: 17-27
  - 33 Takagi K (1966b) Taxonomic and nomenclatural status in chaos of the Gobiid fish, *Chaenogobius annularis* Gill Tomiyama with description of the genus *Rhodoniichtys*, Gen Nov J Tokyo Univ Fish 52: 29-45
  - 34 Takagi K (1967) Topologie du systeme sensoriel cephalique des Gobioides. La Mer 5: 131-145
  - 35 Thorpe J P (1982) The molecular clock hypothesis: Biochemical evolution, genetic differentiation and systematics. Ann Rev Ecol Syst 13: 139-168
  - 36 Thorpe J P (1983) Enzyme variation, genetic distance and evolutionary divergence in relation to levels of taxonomic separation. In "Protein Polymorphism, Adaptive and Taxonomic Significance" Ed by G S Oxford, D Rollinson, Academic Press, London and New York, pp 131-152



## Speciation of Japanese Pond Frogs Deduced from Lampbrush Chromosomes of their Diploid and Triploid Hybrids

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**ABSTRACT**—To examine the hybrid origin hypothesis of *Rana porosa porosa* cytogenetically, the lampbrush chromosomes of triparental allotriploids comprising the genomes of *R. nigromaculata*, *R. p. brevipoda*, and *R. p. porosa* were investigated together with those of their intra- and interspecific hybrids. The behavior of their homologous lampbrush chromosomes provided little evidence that chromosomal material from *R. nigromaculata* is present in the genomic chromosomes of *R. p. porosa*. On the contrary, it is suggested that *R. p. porosa* and *R. nigromaculata* are phylogenetically more distant than are *R. p. brevipoda* and *R. nigromaculata*.

### INTRODUCTION

With respect to the differentiation of *Rana porosa porosa* Cope, Moriya [13] and Kawamura and Nishioka [4-6] proposed the hypothesis of hybrid origin between *R. nigromaculata* Hallowell and *R. p. brevipoda* Ito. This hypothesis was supported by Kuramoto [7], but questioned by Matsui and Hikida [12]. Recently, Nishioka *et al.* [17] offered support for the hypothesis from electrophoretic analysis, though the support was not without a tinge of interested consideration. Although I was a collaborator of the latter paper, I now question the hybrid origin hypothesis in view of the fact that the lampbrush chromosomes of *R. p. porosa* closely resemble those of *R. p. brevipoda*, and yet there are no landmarks derived from *R. nigromaculata* throughout their axes (unpublished).

The hybrid origin should be demonstrated by comparing the behavior of lampbrush chromosomes in diploid hybrids between the above-mentioned three taxa, because the number of chiasmata that control the behavior of lampbrush chromosomes changes in accordance with the extent of similarity between the homologues of parental species [9, 14, 20]. Similarly, when the genomic chromosomes of these three taxa are placed together in an oocyte, provided that *R. p. porosa* receives many dominant and recessive genes from *R. nigromaculata* as suggested by Kawamura and Nishioka [4], some of the chromosomes of *R. p. porosa* should join inevitably to those of *R. nigromaculata* and act as a mediator in formation of trivalents.

The lampbrush chromosomes of *R. nigromaculata* are easily distinguished from those of *R. p. brevipoda* [16] and *R. p. porosa* (unpublished) by size, type, and position of the landmarks. Thus, the lampbrush chromosomes of triparental allotriploid females were examined to cytogenetically determine the relative degree of synaptic affinity among the

chromosomes of these taxa together with those of their intra- and interspecific hybrid females. This paper describes these results and a new hypothesis of the differentiation of *R. p. porosa* is proposed.

### MATERIALS AND METHODS

The female frogs studied are described in Table 1. The parental frogs for crosses were from the lineages of *R. p. brevipoda* collected from Konko, Okayama Prefecture, *R. p. porosa* from Machida, a city of Tokyo, and *R. nigromaculata* from Hiroshima. The frogs were crossed by artificial fertilization. Autotriploid frogs were produced by cooling the fertilized eggs of *R. p. brevipoda* to  $\cong 1^\circ\text{C}$  for 2 hrs. Two kinds of allotriploid frogs were produced by inseminating a few diploid ova which *brevipoda* ♀ × *nigromaculata* ♂ hybrid females spawned with spermatozoa of the two subspecies. Tadpoles were fed on boiled spinach or chard, and frogs were fed on houseflies or tropical crickets.

Lampbrush chromosomes were removed from the ovarian eggs of two-year-old females just prior to hibernation (November) according to Gall's method with a slight modification [1, 20], and examined under a phase-contrast microscope. The abbreviations B, P, and N refer to *brevipoda*, *porosa*, and *nigromaculata* chromosomal sets, respectively. The letters in parentheses indicate the sources of cytoplasm. Chiasma frequencies per oocyte were compared using Student's or Aspin-Welch's *t*-test. Chi-square test also was used for the comparison of chiasma numbers in two kinds of allotriploids.

### RESULTS

#### *Autotriploid (B)BBB*

Lampbrush chromosomes from 60 oocytes were analyzed in detail. All the oocytes contained 39 lampbrush chromosomes consisting of 13 triplets of homologues that belonged to five large chromosomes numbered 1 to 5 and eight small chromosomes numbered 6 to 13. These lampbrush chromosomes formed eight or more trivalents in all the oocytes; it was notable that those of six oocytes formed exclusively 13 trivalents (Table 2). All the chromosomes other than those

TABLE 1. Kind, origin, and number of female frogs used in the present study

Kind	Parental Origin		Number of females
	Female	Male	
Autotriploid (B)BBB (3n=39)	<i>R. p. brevipoda</i>	<i>R. p. brevipoda</i>	5
Allotriploid (B)BBN (3n=39)	<i>brevipoda</i> ♀ × <i>nigromaculata</i> ♂	<i>R. b. brevipoda</i>	5
Allotriploid (B)BPN (3n=39)	<i>brevipoda</i> ♀ × <i>nigromaculata</i> ♂	<i>R. b. porosa</i>	4
Diploid hybrid (P)PB (2n=26)	<i>R. p. porosa</i>	<i>R. p. brevipoda</i>	9
Diploid hybrid (P)PN (2n=26)	<i>R. p. porosa</i>	<i>R. nigromaculata</i>	9
Diploid hybrid (N)NP (2n=26)	<i>R. nigromaculata</i>	<i>R. p. porosa</i>	8
Non-hybrid (P)PP (2n=26)	<i>R. p. porosa</i>	<i>R. p. porosa</i>	11

TABLE 2. Number of oocytes having tri-, bi- and univalents in various combinations in the three kinds of triploids

No. of trivalents	No. of bivalents	No. of univalents	(B)BBB	Kind (B)BBN	(B)BPN
13 (39)	0	0	6		
12 (36)	1 (2)	1 (1)	16		
11 (33)	2 (4)	2 (2)	17		
10 (30)	3 (6)	3 (3)	13		
9 (27)	4 (8)	4 (4)	4		
8 (24)	5 (10)	5 (5)	4		
7 (21)	6 (12)	6 (6)			1
6 (18)	7 (14)	7 (7)			1
5 (15)	8 (16)	8 (8)		1	
4 (12)	9 (18)	9 (9)			2
3 (9)	10 (20)	10 (10)		8	2
2 (6)	11 (22)	11 (11)		12	1
1 (3)	12 (24)	12 (12)		12	4
0	13 (26)	13 (13)		11	6
0	0	39 (39)		2	8
Total			60	46	25

Numbers in parentheses show numbers of lampbrush chromosomes forming tri-, bi-, or univalents.

of the trivalents formed bivalents and univalents of the same number.

The number of trivalents in chromosome Nos. 1 to 13 is presented in Table 3. Of the 655 trivalents, 189 joined three

homologues in juxtaposition by four to 12 chiasmata and rarely by terminal fusions (Fig. 1A). In 359 other trivalents, two of the three homologues were joined by two to eight chiasmata and the rest was joined to one of them by one to three chiasmata, a terminal fusion, or both, in addition (Fig. 1B). In the remaining 107 trivalents, the three homologues were joined in tandem by one or two chiasmata or a terminal fusion (Fig. 1C).

In chromosome Nos. 1, 4, 6-9 and 12, the chiasma frequencies were about 1.5 times higher than those of diploid *R. p. brevipoda* (Table 4). Those of the remainder were slightly lower than 1.5 times. The number of chiasmata in each oocyte was between 35 and 76 (average, 55.0) in total.

#### Allotriploid (B)BBN

Lampbrush chromosomes from 57 oocytes were analyzed. Eleven of these oocytes, an aneuploid one (3n-2) lacking the *nigromaculata* chromosomes of Nos. 2 and 8, and 10 hexaploid ones, were omitted from the analysis. The remaining 46 oocytes contained 39 lampbrush chromosomes consisting of one *nigromaculata* and two *brevipoda* chromosomes in each of the 13 homologue triplets (Fig. 2). These chromosomes formed one to five trivalents in 33 oocytes (Table 2). The remaining 13 oocytes had no trivalents. All the chromosomes other than those of the trivalents formed bivalents and univalents of the same number, or simply univalents; two oocytes contained only 39 univalents.

In 64 of the 65 trivalents, a *nigromaculata* chromosome was always joined to one of the two *brevipoda* chromosomes by one or two chiasmata, a terminal fusion, or both, in addition (Table 3). The remaining one trivalent was seen in chromosome No. 6 and arranged three homologues of, in order, *brevipoda*, *nigromaculata* and *brevipoda*, which were each joined by one chiasma in tandem. On the other hand, in 507 triplets of homologues forming a bivalent and a univalent, the bivalent always consisted of two *brevipoda* chromosomes, and the univalent of a *nigromaculata* chromosome. In the remaining 26 triplets of homologues, they



TABLE 3. Behavior of homologous lampbrush chromosomes in each of the 13 triplets in the three kinds of triploids

Kinds	Chromosome behavior in a triplet	Chromosome no.													Total
		1	2	3	4	5	6	7	8	9	10	11	12	13	
(B)BBB	b-b-b	54	57	58	55	53	46	52	48	46	47	44	44	51	655
	b-b, b	6	3	2	5	7	14	8	12	14	13	16	16	9	125
	Total	60	60	60	60	60	60	60	60	60	60	60	60	60	780
(B)BBN	b-b-n	6	6	4	4	3	11	2	3	6	3	6	7	3	64
	b-n-b						1								1
	b-b, n	38	38	40	40	41	32	42	41	38	41	38	37	41	507
	b, b, n	2	2	2	2	2	2	2	2	2	2	2	2	2	26
	Total	46	46	46	46	46	46	46	46	46	46	46	46	46	598
(B)BPN	b-p-n or p-b-n	3	4	3	4		2	2	4	1	2	1	3	2	31
	b-n-p										1	1			2
	b-p, n	14	12	14	13	17	14	14	12	16	15	15	13	14	183
	b-n,p or p-n,b			1				1	1*	1				1*	5
	b, p, n	8	8	8	8	8	8	8	8	8	8	8	8	8	104
	Total	25	25	25	25	25	25	25	25	25	25	25	25	25	325

The abbreviations b, p, and n indicate *brevipoda*, *porosa*, and *nigromaculata* lampbrush chromosomes, respectively. "-" indicates a connection between two homologues.

\* Joining was effected between *brevipoda* and *nigromaculata* chromosomes.

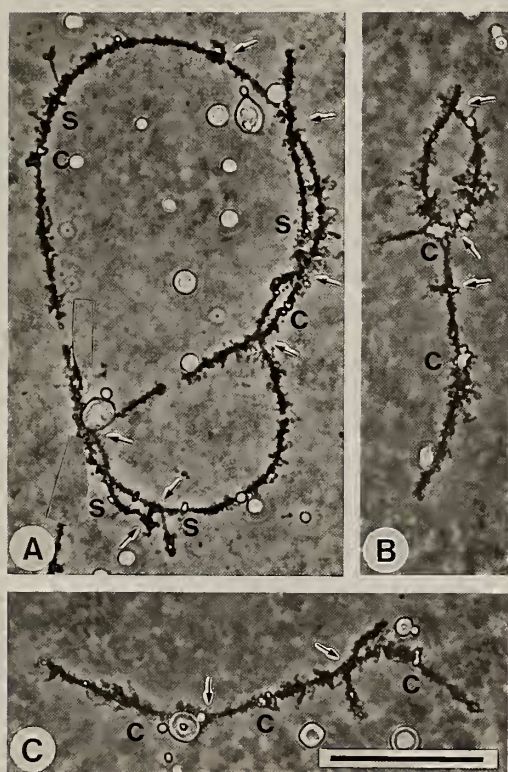


FIG. 1. Microphotographs of trivalents of chromosome Nos. 3 (A) and 10 (B and C) in an autotriploid, (B)BBB. Arrows indicate the positions of chiasmata. c and s represent compound- and simple-type giant loops, respectively. Bar=50  $\mu$ m.

remained as univalents.

In all the trivalents, *nigromaculata* and *brevipoda* chromosomes were joined by 57 (3%) chiasmata in total

except for the terminal fusions. By contrast, joining of two *brevipoda* chromosomes in the bivalents and trivalents was by 2033 (97%) chiasmata in total except for the terminal fusions.

The chiasma frequencies in chromosome Nos. 1 to 13 were about 1.2 times higher than those of diploid *R. p. brevipoda* except in chromosome Nos. 11 and 13, though the chiasmata for *nigromaculata* and *brevipoda* chromosomes accounted for no more than 3% of the total (Table 4). The number of chiasmata in each oocyte was between 0 and 60 (average, 45.4) in total. This average value was different from that of the diploid *R. p. brevipoda* ( $t=3.7$ ,  $P<0.001$ ) or the autotriploid (B)BBB ( $t=4.4$ ,  $P<0.0001$ ).

#### Allotriploid (B)BPN

Lampbrush chromosomes from 41 oocytes were analyzed. Sixteen of the 41 oocytes were seven aneuploid oocytes of  $3n-1$  (three),  $3n-2$  (two), and  $3n-5$  (two), and nine hexaploid oocytes; all of which were omitted from the analysis. In the remaining 25 normal triploid oocytes in which each triplet of homologues consisted of one *brevipoda*, one *porosa*, and one *nigromaculata* chromosomes, the lampbrush chromosomes were somewhat similar in behavior to those of the other allotriploid (B)BBN (Table 2). In 11 oocytes they formed one to seven trivalents, while all the chromosomes other than those of the trivalents formed bivalents and univalents of the same number (Fig. 3). In six other oocytes they formed 13 bivalents and 13 univalents. The remaining eight oocytes had only 39 univalents.

Of the 33 trivalents, 31 joined a *nigromaculata* chromosome to either of the *brevipoda* and *porosa* chromosomes by one or two chiasmata, a terminal fusion, or both, in addition (Table 3). The remaining two trivalents arranged three